Revisiting the von Bertalanffy Seasonal Cessational Growth Function of Pauly et al. (1992)

Derek H. Ogle

April 9, 2016

Introduction

The mean length-at-age for many animals (e.g., CITATIONS) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy (1938)). The parameterization of the VBGF attributable to Beverton and Holt (1957) is most common and may be expressed as

$$L_t = L_\infty(1 - e^{-q}) \qquad (1)$$

with

$$q = K(t - t_0) \qquad (2)$$

where $L(t)$ is the expected or average length at time (or age) t, L_∞ is the asymptotic mean length, K is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980), and t_0 is the theoretical time or age (generally negative) at which the mean length would be zero.

Many animals exhibits seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (CITATIONS). Equation 2 of the traditional VBGF has been modified, usually with a sin function, to model these seasonal oscillations in growth. The most popular of these modifications is from Hoenig and Choudaray Hanumara (1982) and Somers (1988) (and carefully reiterated in Garcia-Berthou et al. (2012)), and uses

$$\begin{aligned} q = &K(t - t_0) \\ &+ \frac{CK}{2\pi} sin(2\pi(t - t_s)) \\ &- \frac{CK}{2\pi} sin(2\pi(t_0 - t_s)) \end{aligned} \qquad (3)$$

where C modulates the amplitude of the growth oscillations and corresponds to the proportional decrease in growth at the depth of the oscillation (i.e., "winter"), and t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point). If C=0, then there is no seasonal oscillation and Equation 3 reduces to Equation 2 and the typical VBGF (Figure 1). If C=1, then growth completely stops once a year at the "winter-point" (WP), whereas values of 0<C<1 result in reduced, but not stopped, growth during the winter (Figure 1).

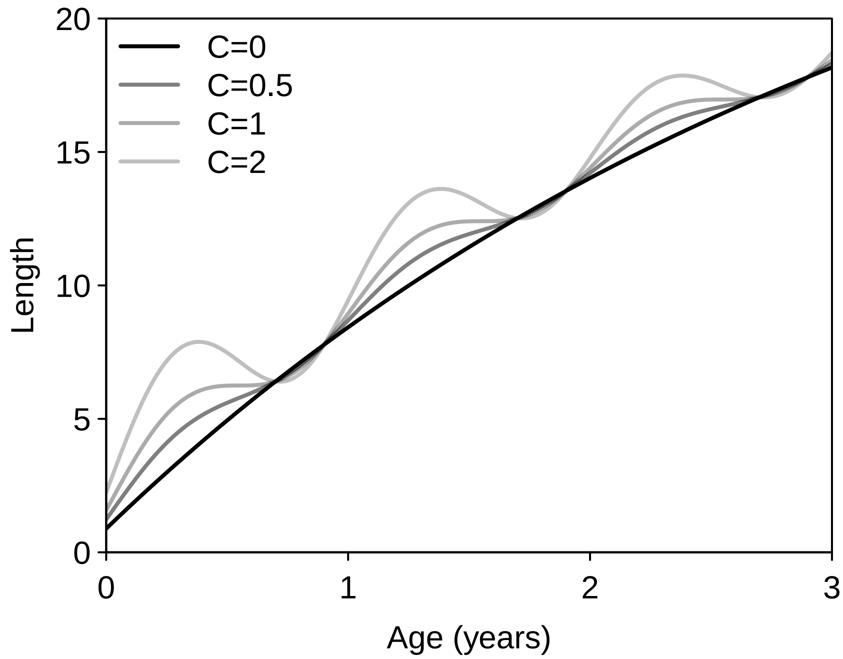


Figure 1: Example VBGF using Equation 3 with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (or WP=0.55), and four different values of C.

Values of C>1 (or <0) in Equation 3 allow seasonal decreases in mean length-at-age (Figure 1). A decrease in mean length is unlikely for organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), although a seasonal decrease in mean length-at-age is possible if size-dependent overwinter mortality occurs (Garcia-Berthou et al. 2012). To address this issue, Pauly et al. (1992) modified Equation 3 to include a true seasonal no-growth period with a smooth transition of the modeled mean length-at-age into and out of the no-growth period. Specifically, their modification is

$$\begin{aligned} q = & K^{'}(t^{'} - t_0) \\ & + \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t^{'} - t_s)\right) \\ & - \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t_0 - t_s)\right) \end{aligned} \tag{4}$$

where NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and $t^{'}$ is found by "subtracting from the real age (t) the total no-growth time occurring up to age t." Furthermore, Pauly et al. (1992) noted that the units on K changed from $year^{-1}$ in Equation 3 to $(1-NGT)^{-1}$ in Equation 4. To eliminate confusion he suggested using $K^{'}$ in Equation 4, as we do here.

Pauly et al. (1992) derived Equation 4 by assuming C=1 (i.e., that the rate of growth is 0 at the WP) and replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the oscillation to the period of growth and noting that $K^{'}$ only operates in this shorter period). Their modification can be described geometrically (though not algorithmically) in two steps. First, the seasonal growth function in Equation 3 with C=1 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using $t^{'}$). The growth trajectory is then separated at the WP and a horizontal segment that is NGT units long is inserted. This forms a growth trajectory that smoothly transitions into and out of a no-growth period (Figure 2).

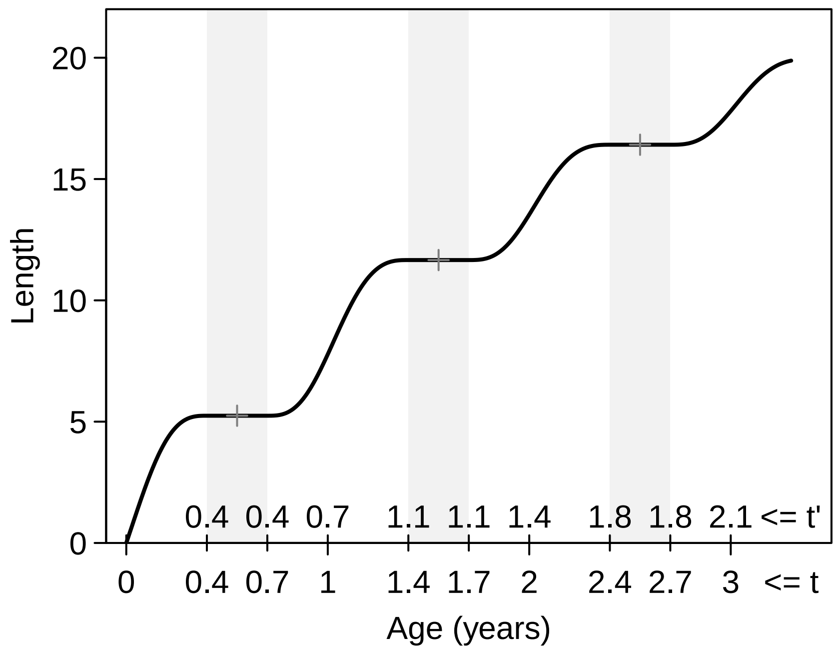


Figure 2: Example VBGF using Equation 4 or Equation 5 with L_∞=30, $K^{'}$=0.428571428571429, t_0=0, NGT=0.3, and t_s=0.05 or WP=0.55. Each no-growth period is marked by a light gray polygon and each WP is marked by the gray plus symbol. The ages adjusted for the NGT (i.e., $t^{'}$) are shown above the x-axis.

Pauly et al. (1992) provided a "diskette" that contained a computer program to estimate the parameters of Equation 4. The diskette is difficult (at best) to obtain and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no description of how $t^{'}$ was operationalized. This is an important step in using Equation 4 because $t^{'}$ is a function of t, but it is also a function of NGT and t_s, which are parameters to be estimated during the model-fitting process. In other words, the values for $t^{'}$ will change with each iteration in the non-linear model-fitting process.

Therefore, the objectives of this note are to (i) describe a function for calculating $t^{'}$ that may be used in the model-fitting process; (ii) describe a slight modification of Equation 4 that eases the calculation of $t^{'}$ while providing a more meaningful parameter; (iii) provide an (open-source) algorithm for the modified function that can be used in model-fitting; and (iv) demonstrate the use of the modified function for fitting length-at-age data.

The Modified Model

In Equation 3, $WP = t_s + \frac{1}{2}$ because the sine function has a period of one year. The growth period is compressed in Equation 4 to be $1 - NGT$. Thus, the start of the no-growth period (SNG) is $t_s + \frac{1-NGT}{2}$. The center of the no-growth period is then $SNG + \frac{NGT}{2}$ or $t_s + \frac{1}{2}$. Thus, $WP = t_s + \frac{1}{2}$ is the center of the no-growth period for Equation 4.

By simple substitution, Equation 4 is modified to include WP rather than t_s.

$$
\begin{aligned}
q = & K^{'}(t^{'} - t_0) \\
& + \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t^{'} - WP - \frac{1}{2})\right) \\
& - \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t_0 - WP - \frac{1}{2})\right)
\end{aligned} \tag{5}
$$

As noted by Pauly et al. (1992) the calculation of $t^{'}$ depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of $t^{'}$ also depends on the position of the no-growth period within a year. Here, the position of the no-growth period is defined by the SNG. However, because the SNG has a one-to-one relation with WP and t_s it can also be defined relative to these parameters.

The following algorithm is used to convert from observed ages (t) to ages adjusted for cumulative NGT prior to age t ($t^{'}$).

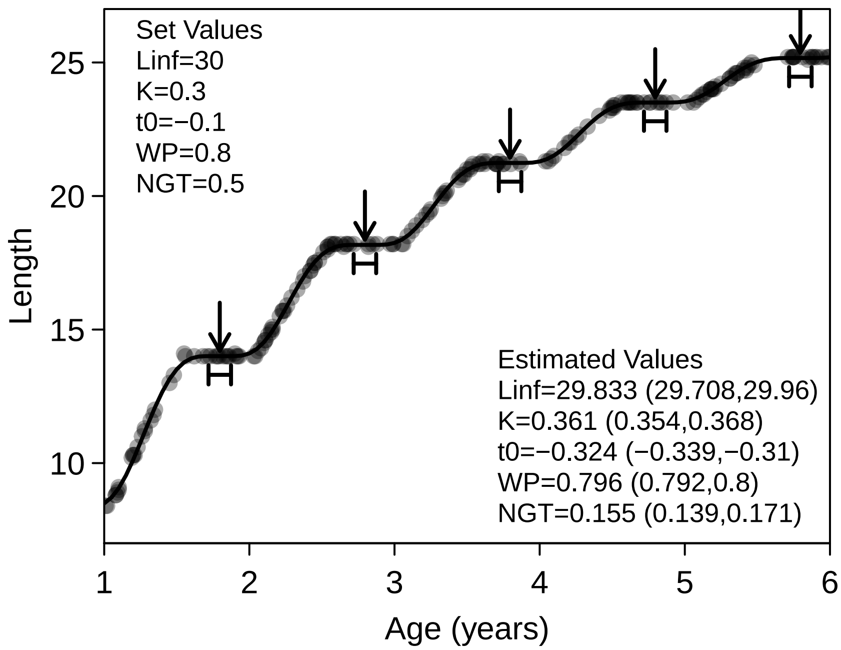
1. Shift the age (t) by subtracting the start of the no-growth period (SNG) from t, such that a whole number age represents the start of a no-growth period. For example, if SNG=0.4, then t=2.4 will become 2.0 and t=2.9 will become 2.5.
2. Subtract the whole number age from the shifted age such that the remaining decimal represents the fraction of a shifted year. For example, a 0 will result if the shifted age is 2.0 and a 0.5 will result if the shifted age is 2.5.
3. Substract the NGT from each of the values from the previous step.
4. If the value from the previous step is negative, then the age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the fraction of a growth period completed.
5. Add the value from the previous step to the total growth time completed (i.e., the product of the number of growth periods completed and the length of the growth period $(1 - NGT)$).
6. Compute t' by adding back the SNG that was subtracted in Step 1.

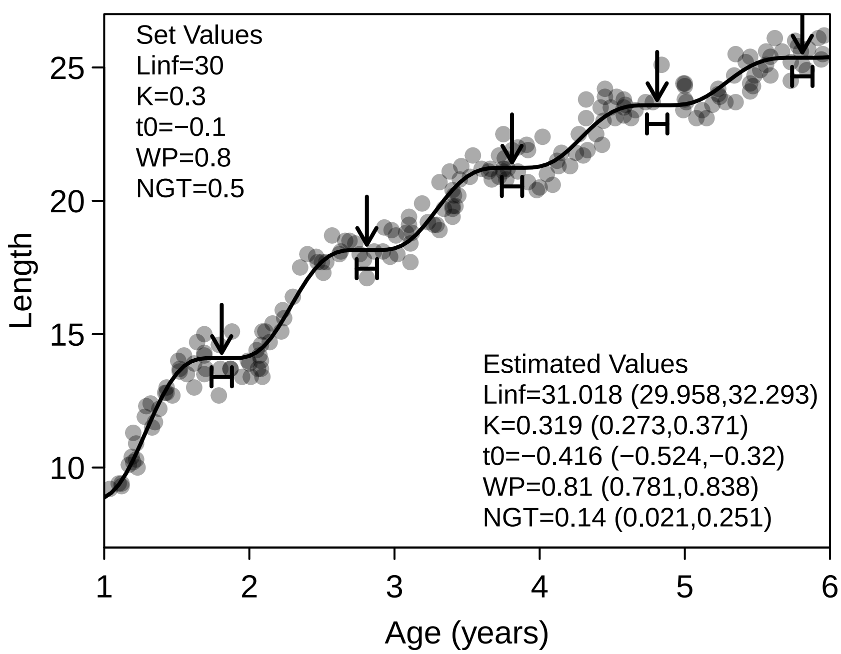
Further examples of $t^{'}$ values relative to t values are shown in Figure 2. This algorithm for computing $t^{'}$ is implemented in an R (R Development Core Team 2016) function as shown in Appendix 1. With this, Equation 6 is easly implemented as an R function as shown in Appendix 2.

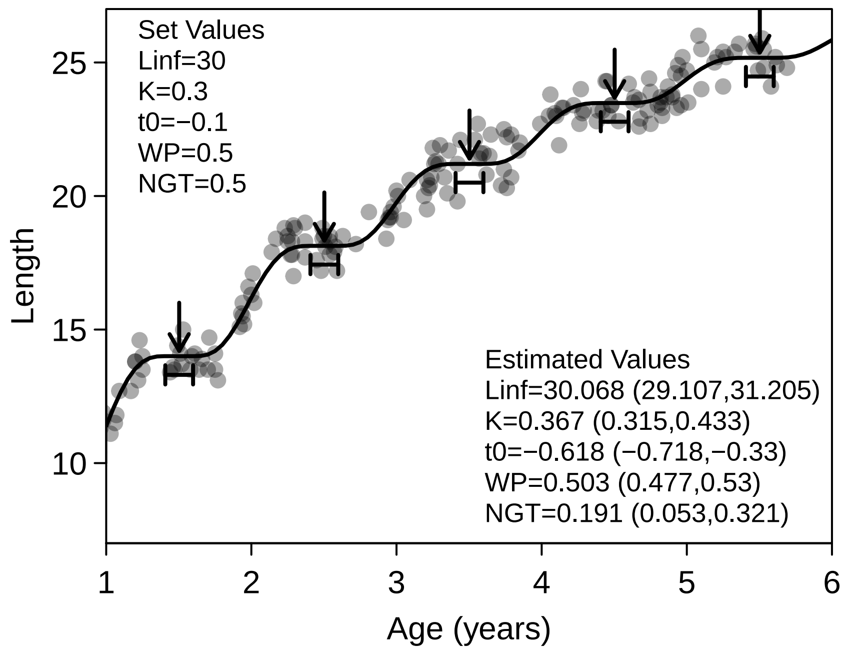
Fitting the Modified Model

Simulated Data

Fish ages (including fractions of a year) and lengths at capture were simulated with vbDataGen() from the FSAsims package (CITATION) in R. In this application, this functions simulates seasonal fish growth with the following steps:


Set Values
Linf=30
K=0.3
t0=−0.1
WP=0.8
NGT=0.5
Estimated Values
Linf=29.833 (29.708,29.96)
K=0.361 (0.354,0.368)
t0=−0.324 (−0.339,−0.31)
WP=0.796 (0.792,0.8)
NGT=0.155 (0.139,0.171)
Length
Age (years)


Set Values
Linf=30
K=0.3
t0=−0.1
WP=0.8
NGT=0.5
Estimated Values
Linf=31.018 (29.958,32.293)
K=0.319 (0.273,0.371)
t0=−0.416 (−0.524,−0.32)
WP=0.81 (0.781,0.838)
NGT=0.14 (0.021,0.251)
Length
Age (years)



Real Data

Discussion

Appendices

Appendix 1

```
##################################################################################
## internal function to compute t-prime
##################################################################################
iCalc_tpr <- function(t,WP,NGT) {
  ## Step 1
  SNG <- WP-NGT/2
  tmp.t <- t-SNG
  ## Step 2 (in parentheses) and Step 3
  tmp.t2 <- tmp.t-floor(tmp.t) - NGT
  ## Step 4
  tmp.t2[tmp.t2<0] <- 0
  ## Step 5 (in parentheses) and Step 6 (also returns value)
  (floor(tmp.t)*(1-NGT)+tmp.t2) + SNG
}
```

Appendix 2

```
##################################################################################
## Main Function
##   Linf, t0 as usual
```

```
##   Kpr = K-prime as defined in Pauly et al. (units are diff than usual K)
##   WP = "Winter Period" (middle point of no-growth period) = ts+0.5
##   NGT = "No Growth Time" = "fraction of a year where no growth occurs"
##   tpr = "t-prime" = actual age (t) minus cumulative NGT prior to t
################################################################################

VBSCGF <- function(t,Linf,Kpr=NULL,t0=NULL,WP=NULL,NGT=NULL) {
  if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]
  WP <- Linf[[4]]; NGT <- Linf[[5]]
  Linf <- Linf[[1]] }
  tpr <- iCalc_tpr(t,WP,NGT)
  q <- Kpr*(tpr-t0) +
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(tpr-WP+1/2)) -
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(t0-WP+1/2))
  Linf*(1-exp(-q))
}
```

References

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Page 533. United Kingdom Ministry of Agriculture; Fisheries.

Garcia-Berthou, E., G. Carmona-Catot, R. Merciai, and D. H. Ogle. 2012. A technical note on seasonal growth models. Reviews in Fish Biology and Fisheries 22:635–640.

Hoenig, N., and R. Choudaray Hanumara. 1982. A statistical study of a seasonal growth model for fishes. Tehcnical Report, Department of Computer Sciences; Statistics, University of Rhode Island.

Pauly, D., M. Soriano-Bartz, J. Moreau, and A. Jarre-Teichmann. 1992. A new model accounting for seasonal cessation of growth in fishes. Australian Journal of Marine and Freshwater Research 43:1151–1156.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing, v3.3.0. R Foundation for Statistical Computing, Vienna, Austria.

Schnute, J., and D. Fournier. 1980. A new approach to length-frequency analysis: Growth structure. Canadian Journal of Fisheries and Aquatic Sciences 37:1337–1351.

Somers, I. F. 1988. On a seasonally oscillating growth function. Fishbyte 6(1):8–11.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.